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studies in this group. Moreover, the number of species included in the Rhizinaceae is not large, and collections of some of these are rarely made (UNDERWOOD 29, HONE 22, BURT 6).

During the summer of 1914 the writer discovered an abundant supply of the apothecia of Rhizina undulata, and was able to collect numerous very young fruit bodies in addition to the older stages. These have furnished all the necessary material for a thorough study of the development of the fruit body in this species. Rhizina undulata is particularly suitable for investigation, since it is the type of the genus and family, and probably the best known member of the group. SCHRÖTER (27) separates the Rhizinaceae from the Geoglossaceae and Helvellaceae on the basis of the sessile fruit body. BOUDIER (3), attempting to arrange the Discomycetes in a natural classification, has developed a system very different from that of SCHRÖTER. He makes his primary separation on the basis of the method of rupture of the ascus. He places in one large group (Operculés) those forms whose asci open by an apical lid, and in the other group (Inoperculés) those whose asci open merely by a pore. By this separation the Helvellaceae and Rhizinaceae fall in the first group and the Geoglossaceae in the second. BOUDIER regards the Rhizinaceae as more closely related to such genera as Peziza, Aleuria, and Sarcoscypha of the Pezizales than to either the Helvellaceae or Geoglossaceae. LAGARDE (23) makes the primary separation also on the method of rupture of the ascus. The facts brought out in the study of the development of the fruit body in various genera of the Discomycetes are especially interesting for the bearing they have on the questions involved in these two opposing systems of classification. The present investigation is undertaken with the hope that more complete information with reference to ontogeny will render less difficult the consideration of the phylogeny of the group.

#### Rhizina undulata Fr.

HISTORICAL.—The genus *Rhizina* was founded by FRIES (16) in 1815. It is characterized by the possession of prominent ropelike strands of mycelium, termed rhizoids. These are developed

in considerable numbers on the lower surface of the fruit body, and serve to attach it to the substratum. Representatives of this genus, therefore, are not easily mistaken.

Rhizina undulata was apparently first described by SCHAEFFER (26) under the name Elvela inflata. This writer published a colored figure of the plant which illustrates well the more evident characters of the species. FRIES (16) later described the fungus as Rhizina undulata, and discusses it under this name in Systema mycologicum (17). In accordance with the international rules of botanical nomenclature the writer designates the species by this name, but it has more commonly been referred to in recent literature as Rhizina inflata. The plant has been described by many writers and has frequently been figured. Excellent colored plates are given by BOUDIER (2). On account of the fact that the fungus is parasitic on the roots of certain trees its morphology and life history have received considerable attention (TUBEUF 28).

HARTIG (19, 20, 21) discusses at some length the structure of the mature fruit body. He made no attempt to study its development. More recently WEIR (30) has published photographs of apothecia with notes on the parasitism of the fungus. None of these workers describes other than the mature condition. MATERIAL AND METHODS.—The apothecia used by the writer in these investigations were collected in July 1914 in a small pine wood north of Beebe Lake near the Cornell University campus at Ithaca, New York. Due to favorable weather conditions the truit bodies were developing in great profusion, and dotted the ground throughout a considerable portion of the wood. Although no attempt was made to obtain corroborative evidence as to the parasitism of the species, it was noted that the fruit bodies in many cases were firmly attached to the roots of living pines. Transverse sections through pine rootlets will be noted in the accompanying plates. In fact, the youngest fruit bodies were obtained more easily by tearing up a superficial root invested with wefts of mycelium on which the young fruit bodies were being differentiated. In this manner immature fruit bodies in all stages of development were obtained easily. Mature apothecia were available in such abundance that several quart jars of material were preserved for class

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use. The writer's determination of the fungus was confirmed independently by E. J. DURAND and F. J. SEAVER, and his thanks are due both of these gentlemen.

The young apothecia collected for the study of the development of the fruit body were immediately placed in medium strength chromo-acetic acid fixer. They were carried into paraffin, and were studied in serial sections of  $4-7\mu$  thickness. The material was stained chiefly with Heidenhain's iron alum-haematoxylin, no counter stain being used. For certain of the more mature stages the shortened Flemming's triple stain proved more useful. The material was sectioned and stained in the laboratories of the Brooklyn Botanic Garden in the summer of 1915, while the writer held a visiting fellowship at that institution. He wishes to take this opportunity to express his appreciation of the courtesy of Director C. S. GAGER in extending to him the facilities of the laboratories, and to acknowledge his indebtedness to Dr. E. W. OLIVE for many kindnesses, including several helpful suggestions concerning technique. The investigation was carried to completion in the laboratories of the Department of Plant Pathology at

## Cornell University.

THE MATURE FRUIT BODY.—The mature apothecia exhibit great variation in size and shape. Considerable irregularity of contour is characteristic, and the early fusion of several fruit bodies results at maturity in large unsymmetrical structures. The apothecia shown natural size in fig. I illustrate well the extent of variation. The two fruit bodies in the lower left hand corner of the figure were inverted to reveal the clusters of ropelike rhizoids which give to the genus its name. The fruiting surface varies from a rich chestnut to a dark brown, and when moistened is peculiarly sticky and glutinous. Around the margin of the apothecium a sterile zone is indicated by a narrow, white, encircling band which contrasts sharply with the brown hymenium. This white margin is

very evident in all stages. In the youngest fruit bodies the entire surface is white, the brown fruiting layer later making its appearance at the center and increasing rapidly in extent. The smaller of the fruit bodies pictured in fig. I show this condition clearly.

THE HYMENIUM.—The hymenium at maturity contains 3 types of structures: asci, paraphyses, and paraphysis-like structures which the writer will designate as setae, since they arise far below the hymenium, and are dark colored and thick-walled. The asci are narrow, cylindrical to clavate, and 8-spored. The spores are uniseriate, fusiform, hyaline, unicellular, and at maturity biguttulate. The paraphyses are filamentous, unbranched, multiseptate, hyaline, and at the apex distinctly clavate. The setae are heavy-walled, brown, non-septate, unbranched tubes originating far below the hymenium (fig. 11) and discharging a brown sticky secretion at their tips. This secretion flows over the surface of the hymenium made up of the swollen tips of the paraphyses, and gives a condition superficially resembling an epithecium. HARTIG (20, 21) states that it is impossible to procure a pure culture from the spores of this fungus on account of the bacteria which swarm in myriads in this glutinous secretion and find their way down between the paraphyses. These bacteria induce a rapid decay of the entire apothecium, and give to it in age a peculiar water-soaked, brittle consistency. In fig. 13 a portion of the hymenium is shown at a stage approximating maturity. The broad, deep-staining tubes are the setae. Surrounding these are the paraphyses, and pushing up from below may be seen the young, uninucleate asci. The swollen tips of the paraphyses are obscured by the layer of deep-staining glutinous material. MYCELIUM.—The mycelium of Rhizina undulata possesses more than ordinary interest for the systematist. It is described by HARTIG (21) as bearing clamp connections. He says: "Although I have much diffidence in maintaining that this feature, which otherwise is peculiar to the Hymenomycetes, is characteristic of. this parasite, still I cannot doubt that these filaments with clamp cells belong to it." The writer has given the mycelium careful examination, and has been unable in his collections to find clamp connections on hyphae certainly belonging to the fruit bodies of Rhizina. He does not feel, however, that sufficient investigation of this point has been carried on to enable him to state definitely that they never occur. The mycelium develops profusely, and covers the soil particles and small rootlets as a whitish, moldlike

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growth. Upon this subiculum compact masses of hyphae develop as minute, snow white knobs. These represent the primordia of fruit bodies.

DEVELOPMENT OF THE ASCOCARP.—The youngest fruit body sectioned measures slightly less than 0.3 mm. in lateral diameter. A considerable number of others possess a maximum diameter of 1 mm. or less. The youngest fruit body studied (fig. 2) is a wholly undifferentiated "button" of mycelium. The hyphae making up the primordium arise in this case from about a small rootlet, and pushing upward between other rootlets run more or less distinctly parallel toward the surface of the ground, where they radiate in every direction, giving the primordium its rounded form. At this early stage there is no indication of sexual cells, and no evidence other than shape that this "button" of mycelium is to develop into a fruit body.

The hyphae at the surface of the primordium form a more or less definite palisade layer, although at this early period they are sufficiently flexuous to destroy the very definite palisade effect evident later. These hyphae in many cases can be traced backward with ease to the point of origin of the fruit body. No structure of the nature of an enveloping veil is present, and it is incredible that one could have existed at an earlier period. Neither in this nor in any later stage has the writer been able to find remnants of a ruptured envelope such as that figured by McCUBBIN (25) for Helvella elastica. He has searched for these in sections of many very young fruit bodies and is absolutely convinced that in Rhizina undulata the ascocarp is at no stage provided with a veil. The fruit body is therefore gymnocarpous and the hymenium is "exposed from the first." Fig. 2 shows in median longitudinal section a fruit body of Rhizina undulata considerably younger than the youngest stage photographed by MCCUBBIN in Helvella. The deep-staining spots at the side and base of the primordium are

transverse sections of pine rootlets.

MCCUBBIN states that in *Helvella elastica* "the envelope which covers the fruiting body in its early stages arises from the palisade layer. Many of the club-shaped hyphae of the latter continue to grow out beyond the general surface, then turn at right angles,

and interlacing in every direction along the surface form a matted web 2-8 threads in thickness. This membrane is very transitory, however, and undergoes degeneration at an early period. . Its protoplasm takes on a granular appearance, the cell outlines become indistinct, and finally the whole disintegrates into a deeply staining mass in which the nuclei are the most prominent feature. Long before the process is complete, however, the rapid growth of the underlying tissue bursts the envelope so that it adheres in flakes (figs. 57, 58). Then the paraphyses and intercalary palisade hyphae pushing out to the surface complete the separation and all traces of it are cast off." It is to be regretted that MCCUBBIN did not publish photomicrographs of stages younger than that shown in his fig. 57. If in Helvella, as he states, the envelope, which incloses the fruit body in the early stages, arises from the palisade layer, it might be concluded that the section of Rhizina undulata shown in fig. 2 is too young to possess the envelope, and that it might logically be expected to develop later on older fruit bodies. That it does not do so, however, is certain. The writer has had available a sufficiently large number of fruit bodies in all stages of development to preclude any misinterpretation with reference to this point. No veil or fragment of a veil has been found on any of the fruit bodies sectioned. Figs. 3-6 show median longitudinal sections through primordia somewhat older than that pictured in fig. 2. The magnification in the 5 cases is the same, being 40 diameters. Other fruit bodies sectioned, of intermediate sizes, bring out no additional facts. In fig. 3 the palisade nature of the hyphal arrangement at the periphery is evident. The deep-staining area on the upper surface to the left of the center is a fragment of a sectioned rootlet other portions of which were cut away in trimming the print. Other sections of similar rootlets appear at different places in the interior of the fruit body. At the base of the ascocarp can be noted the tendency of the mycelium to form thick rhizoids. These young rhizoids appear in section in figs. 3, 5, and 6. Fig. 5 shows the palisade layer of hyphae very clearly. In fig. 10 a portion of the palisade layer of a fruit body approximately the same age as that

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in fig. 5 is shown much enlarged. It will be noticed here that the tips of the hyphae at the periphery stain very deeply. This is probably due to the fact that, since growth is taking place much more rapidly at the tips of the hyphae, the protoplasm at this point contains as the result of metabolism more deeply staining contents. In certain young fruit bodies (fig. 4) the setae are developed much earlier than in others. The reason for this is not known. They are prominent organs, originate from the deeper lying tissue of the fruit body, and protrude beyond the palisade layer as deepstaining spines. These are shown much enlarged in fig. 14. It will be noted that they are of much greater diameter than the other hyphae of the ascocarp. They arise as differentiations of ordinary vegetative hyphae. SEXUALITY.—Near the center of the sections shown in figs. 3 and 5 are to be seen deep-staining elements. These bodies constitute the sexual apparatus of the fungus, and at a somewhat later stage (fig. 9) give rise to the ascogenous hyphae. Since the writer is engaged in the preparation of another paper dealing with the details of the sexual process in Rhizina undulata, he will refrain from further comment on these structures at this point. PARAPHYSES.—The layer of paraphyses is developed comparatively early in the history of the fruit body and constitutes a well defined zone long before the asci are produced. Fig. 7 shows a median longitudinal section through a young apothecium on the upper surface of which the layer of paraphyses is being differentiated. In fig. 8 this same layer is shown more highly magnified. The paraphyses arise from the ordinary hyphae in the interior of the fruit body, and are in reality a specialized portion of the palisade layer. As the fruit body enlarges by the elongation and branching of the hyphae at the periphery, those palisade hyphae which lie on the upper surface increase in number, run more nearly parallel, and come to stand very close together. They soon constitute a well defined zone, the individual units of which appear straighter, slightly narrower, and many times more abundantly septate than the palisade hyphae covering the remainder of the fruit body. This layer of paraphyses continues to develop at the margin as the fruit body increases in diameter, the line of demarcation between

paraphyses and palisade hyphae at the point of contact never being very sharp. Fig. 9 pictures approximately one-half of a median longitudinal section through an older fruit body in which the layer of paraphyses has become sharply differentiated from the tissue of the fruit body below. The rounded sterile margin of the apothecium is here evident.

ASCOGENOUS HYPHAE.—Immediately beneath the paraphyses is

a deeper-staining zone filled with the ultimate tips of the profusely branching ascogenous hyphae. These hyphae have their origin near the base of the fruit body in the sexual apparatus previously mentioned, and may be seen ramifying throughout the interior of the ascocarp as they branch and rebranch on their upward journey toward the hymenium. At this stage these threads have not yet undergone crozier formation at their tips, and no young asci are present. Fig. 12 shows a section through the hymenium of a more mature apothecium in which the young asci are pushing up among the paraphyses. The septate paraphyses, the tubular setae, and the young, deep-staining, clavate asci show here to good advantage. In fig. 13 the asci are shown at about one-half their mature size, and the fusion nucleus may clearly be seen in each. In this and other sections the deep-staining glutinous secretion previously discussed forms a well defined layer above the clavate tips of the paraphyses.

## General considerations

The results of the present investigation on the origin and development of the ascocarp in *Rhizina undulata* are particularly interesting in the light of the facts disclosed by various workers on other allied forms. Before the publication of the work of DITTRICH (**10**) on the development of *Leotia lubrica* and *Mitrula phalloides*, it was generally assumed that in the 3 families of the Helvellales the fruit body is gymnocarpous. After the appearance of DIT-TRICH's paper the pendulum of opinion swung to the other extreme, and we find the statement made by DURAND (**14**) that in his opinion "when the development of the Discomycetes shall be better understood it will be found that in none of them, not even in the Helvellaceae, is the hymenium 'exposed from the first.'" It is evident now from the results of researches on various

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Geoglossaceae that certain members of this family are at first provided with a veil. It is equally certain that in Rhizina undulata no enveloping membrane is ever present. Both conditions occur therefore within the order. Whether it will prove possible to separate the families of the orders on the basis of the presence or absence of a veil is doubtful, but additional investigations on members of the 3 families will be necessary to determine this point. Since the work of MCCUBBIN (25) on Helvella elastica is the only contribution of any importance to our knowledge of the development of the fruit body in the Helvellaceae, it is desirable that other representatives of this family be studied. Also, since MCCUBBIN has stated definitely "from observations on a very complete series of stages that Geoglossum hirsutum shows no trace whatever" of a veil, it is desirable that photographs be published demonstrating the gymnocarpous nature of the ascocarp in this or other members of the Geoglossaceae in which a veil is absent at all stages. Finally, the development of the fruit body in additional species of the Rhizinaceae should be studied to determine whether the conditions described for Rhizina undulata are typical of the

entire family.

It has become increasingly evident since the publication by SCHRÖTER (27) of his system of classification of the Discomycetes that his basis for the separation of the Helvellales from the other orders of the group is untenable. Not only has it been demonstrated that in certain of the Helvellales the fruit body is angiocarpous, but also in the Pezizales it has been shown that certain species possess a fruit body which is clearly gymnocarpous. As representatives of this latter group may be enumerated Ascodesmis (CLAUSSEN 8), Pyronema confluens (HARPER 18, CLAUSSEN 9, et al.), Lachnea stercorea (FRASER 15), L. scutellata (BROWN 5), and Ascobolus magnificus (DODGE II, I2, I3). The presence or absence of a hyphal envelope, therefore, cannot be used to separate the Helvellales and Pezizales as constituted by SCHRÖTER, and some other system of classification of the Discomycetes must be employed. That of BOUDIER (3) has met with considerable favor. As pointed out by DODGE (13) and ATKINSON (1), several well defined types of ascocarps are present in the Ascomycetes, and these

should be considered in any system of classification. The somewhat loose use of the terms "angiocarpous" and "gymnocarpous" and of the phrase "hymenium exposed from the first" has resulted, however, in some confusion. In some species (for example Leotia *lubrica*) the ascocarp is at the beginning inclosed by an envelope which is transitory and disappears before the hymenium is formed, while in others (for example, Rhizina undulata) it lacks at all stages any indication of a veil. In both cases the hymenium is "exposed from the first," but the development of the fruit body is essentially different, and if the veil has any phylogenetic significance the two forms cannot be regarded as closely related. DODGE (13) states that "the real question as to whether an ascocarp is to be classed as open or closed in its early stages depends upon whether the young hymenial layer arises endogenously, as in Ascobolus furfuraceus, or is from the first free and exposed, as in Pyronema." It seems to the writer of greater significance to determine whether the ascocarp is itself at any stage inclosed by an envelope. This is certainly true from the standpoint of phylogeny.

#### Summary

1. The mycelium of *Rhizina undulata* Fr. spreads among the soil particles, and covers the smaller rootlets of pines and other trees, forming a whitish moldlike growth. Upon this subiculum compact masses of hyphae develop as minute, snow white, rounded knobs. These constitute primordia of ascocarps.

2. The ascocarp primordium in the youngest stages shows no evidence of a sexual apparatus. It is made up of undifferentiated hyphae, which at its surface form a palisade layer.

3. The ascocarp is neither at the beginning nor at any subsequent period provided with a hyphal envelope. The fruit body is therefore gymnocarpous and the hymenium is "exposed from the first."
4. There is developed in the interior of the young ascocarp a

well defined sexual apparatus from which the ascogenous hyphae arise. The details of the sexual process have been studied and will be described in a later paper.

5. The ascogenous hyphae branch repeatedly and undergo crozier formation in the development of the young asci.

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6. The paraphyses are a differentiation of the palisade layer which covers the fruit body at all stages.

7. In the ascocarp of this species there are present paraphysislike structures which arise early in the history of the fruit body. They are non-septate, thick-walled tubes which originate far down in the hypothecium, traverse the hymenium, and discharge a brown, glutinous secretion at their tips. The writer has applied to these the term "setae."

8. At maturity the ascocarp is variable in size and shape. The brown hymenium is bordered by a sterile white margin.

9. There are present on the lower surface of the ascocarp numerous prominent rhizoids.

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#### EXPLANATION OF PLATES XVII AND XVIII

FIG. 1. Rhizina undulata Fr., natural size, Ithaca, New York, July 1914; group of apothecia selected to show variation in size and shape; note sterile white margin on both young and old plants, and tendency for adjacent fruit bodies to fuse; at lower left hand corner of figure 2 apothecia are inverted to show lighter colored, lower surface and dense clusters of stout rhizoids which serve to attach the fruit body to substratum.

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FIG. 2.—Median longitudinal section through a very young ascocarp primordium,  $\times 40$ ; note pine rootlets in section at side and base.

FIG. 3.—Median longitudinal section through a somewhat older fruit body, X40; deep-staining body at periphery above is fragment of section

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through a pine root such as those shown in the lower half of fruit body; deepstaining structures near center of section are sexual cells which later give rise to ascogenous hyphae; at base young rhizoids are shown in section.

FIG. 4.—Median longitudinal section through a young fruit body in which setae have developed early,  $\times 40$ ; these may be seen projecting above layer of palisade hyphae.

FIG. 5.—Median longitudinal section through a young fruit body,  $\times 40$ ; palisade layer of hyphae at periphery shows plainly; note sexual cells at center of section.

FIG. 6.—Median longitudinal section through a slightly older fruit body,  $\times 40$ .

FIG. 7.—Median longitudinal section through a somewhat older fruit body in which the layer of paraphyses is being differentiated from palisade layer,  $\times 29$ .

FIG. 8.—Layer of paraphyses shown in fig. 7 enlarged to show structure more clearly,  $\times 40$ ; note indefinite line of demarcation between layer of paraphyses and palisade layer of sterile margin.

FIG. 9.—Approximately one-half of a median longitudinal section through considerably older fruit body,  $\times$  32; note well defined layer of paraphyses, sterile margin, and definite, deep-staining zone below the paraphyses made up of tips of ascogenous hyphae; ascogenous hyphae can be seen originating near base of apothecium and branching profusely as they ramify throughout

the fruit body and approach hymenium.

FIG. 10.—Portion of section such as presented in fig. 5 enlarged to show structure of palisade layer,  $\times 192$ ; note deep-staining tips of hyphae.

FIG. 11.—Longitudinal section through young hymenium of fruit body of about the same age as that shown in fig. 9,  $\times$  192; note numerous prominent setae originating below hymenium; note also deep-staining layer at tips of paraphyses, resulting from glutinous secretion poured over hymenium by setae.

FIG. 12.—Longitudinal section through immature hymenium of fruit body somewhat larger than that shown in fig. 9,  $\times$  192; note slender, septate paraphyses, prominent tubular setae, and young deep-staining asci.

FIG. 13.—Longitudinal section through hymenium of fruit body approaching maturity,  $\times 192$ ; asci have not yet formed spores; fusion nucleus is visible in some cases.

FIG. 14.—Portion of section given in fig. 4 enlarged to show setae at margin of fruit body,  $\times 192$ ; note that they are much larger in diameter and more deeply staining than the hyphae of palisade layer.

## BOTANICAL GAZETTE, LXIII

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PLATE XVII



# FITZPATRICK on RHIZINA



